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Post-reproductive changes in female crab spiders (*Misumena vatia*) exposed to a rich prey source

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Abstract. Life history theory predicts that the intensity of selection will decline as individuals age; thus, adaptive traits should decrease during post-reproductive stages. To test this prediction, I measured several potential fitness variables in adult female crab spiders [*Misumena vatia* (Clerck 1757): Thomisidae]: maximum mass before laying, mass after laying, mass at release into hunting site, carapace width, and days since egg-laying upon A) daily rate of loss in mass after egg-laying while guarding a brood and B) daily rate of gain in mass after release into a rich hunting site. These individuals were members of a normally semelparous population guarding their nests without feeding for 1–26 days past egg-laying. Rate of decline in mass of the spiders slowed significantly over time ($P < 0.01$), and large individuals lost mass relatively faster than smaller ones ($P < 0.05$), but no other tested variables affected their rate of loss in mass. However, none of the above-noted variables significantly affected their rate of gain in mass after release into the hunting site. None of these individuals likely produced a second brood. The scarcity of relationships among variables measured, especially those following release into the rich hunting site, is consistent with these individuals experiencing little or no direct selection for fitness-enhancing traits subsequent to egg-laying. The exceptions noted for the guarding period probably resulted directly from success at an earlier life stage.

Keywords: Dispersal, gain in mass, nest-guarding, semelparity, senescence

Life history theory holds that the expected future reproductive success (reproductive value) of individuals declines with age, with selection consequently weakening over time (Fisher 1930; Williams 1957). This state of affairs likely presents a potent force driving populations toward obligate semelparity (reproducing only once) (Roff 1992; Stearns 1992). Following reproduction, a semelparous individual should experience no further selective pressure favoring subsequent survival or reproduction, constrained only by possible responsibilities to its offspring (egg-guarding, defense of young, etc.) (Packer et al. 1998). Thus, such an individual may exhibit a decrease in adaptive patterns as its responsibilities to its young decrease. Fisher maintained that even factors such as parental care usually remain unimportant relative to the main effects of a single large reproductive effort. According to this argument, parents should expend all available resources on direct reproductive output (gametes) at the expense of parental care. Indeed, some species, such as the often-cited Pacific salmon *Oncorhynchus* spp. (Willson 1997), expend so many of their resources immediately prior to and at reproduction that they die soon afterward.

Facultatively semelparous individuals lie intermediate to obligately semelparous and iteroparous conditions and may provide excellent insights into the question of whether to invest in a single brood or to attempt a second. Facultatively semelparous forms include Condition 1) individuals able to replace an initial brood lost part way through the normal period of care (Schneider et al. 2003; Futami & Akimoto 2005), in which case only a single brood survives; and Condition 2) individuals that usually lack the time to produce a second brood (e.g., a short season), though physiologically capable of doing so (Tallamy & Wood 1986; Morse 1994; Schneider et al. 2003). Given the uncertainty associated with Condition 2, individuals of species that guard their broods may confront the important decision of whether to continue guarding, thereby enhancing the survival of their young (Morse 1988a, 1992) or to gamble that by abandoning their first brood to its own devices so they can successfully rear a second brood.

Crab spiders *Misumena vatia* (Clerck 1757) (Thomisidae) provide a particularly favorable opportunity to investigate the relative advantages of guarding young and producing a second brood. In coastal Maine, USA, *Misumena* lay a single brood under normal field conditions and exhibit an extremely high reproductive effort (Fritz & Morse 1985), yet when supplementally fed so that they overcome severe seasonal time constraints resulting from foraging under unpredictable conditions (Morse & Fritz 1982), they may produce second broods (Morse 1994). Further, they exhibit occasional signs of attempting to produce a second brood under natural circumstances at our study sites (Morse 1994). Although the short season probably prevents them from producing a successful second brood if not supplementary fed, almost half of them abandon their brood before the young emerge from the nest. Some of the individuals that leave their broods hunt voraciously and gain considerable mass if they find a satisfactory hunting site, and occasionally will even build and guard second nests, none of which to date have contained eggs (Morse 1994, unpublished data).

Two factors that should favor production of a second brood are minimizing loss of mass while guarding their eggs (after laying) and, especially, maximizing gain in mass after leaving their eggs. Variables likely to affect these two factors include maximum mass before laying, mass immediately after laying, mass at subsequent release into a foraging site, skeletal body size (carapace width), and number of days guarding after laying.

Here I evaluate the hypothesis that post-reproductive responses (after egg-laying), acting through the variables outlined immediately above, maximize an individual's opportunity to rear a second brood. If second broods are to succeed, I predict that some or all of these five independent variables will differ in ways that allow the spiders to enhance fitness, either by minimizing loss in mass or by maximizing rate of gain in mass after egg-laying. Earlier work demonstrated that most females retain adequate sperm to fertilize a second brood (Morse 1994), so failure to mate after their first brood should not impede them from producing a fertile second brood.

To test predictions A and B and to evaluate the role of several variables, I measured loss in mass from egg-laying until release into a hunting site. These individuals had no access to food after egg-laying. Although that starvation regime may appear extreme, post-reproductive guarding *Misumena* seldom capture prey since they usually nest where few insects visit (Morse 1987). I then measured the spiders' rate of gain in mass after their release into the rich hunting site.

METHODS

Study site.—I carried out this study in the summers of 2001–2007 at the Darling Marine Center, South Bristol, Lincoln County, Maine (43.57°N, 69.33°W), in a 3.5 ha field containing several forbs that provide hunting sites for the spiders when the flowers are in bloom. I have described this field in detail elsewhere (Morse 2007). Voucher specimens from this population of *M. vatia* have been deposited in the American Museum of Natural History, New York.

Spiders were released in a dense patch of wild marjoram *Origanum vulgare* of 2.1 m^2 area and 400 flowering stems located in the middle of this field. Their stems varied between 0.4 and 0.6 m in height and bore several small, terminal pinkish-purple (= light mauve: Smithe 1975) flowers in rounded panicles. These flowers bloomed profusely for several weeks from mid-July to early September. The patch attracted large numbers of potential prey for the spiders: bumblebees, butterflies of several species, sarcophagid and tachinid flies, and much smaller numbers of several other insect groups. During the study, only goldenrods *Solidago canadensis* flowered within several meters of the study area, none closer than one meter. Vegetation within a 1-m arc about the marjoram consisted of various grasses and low pasture rose bushes *Rosa carolina* that had completed flowering before the marjoram began to bloom. Thus, the site offered no nearby attractions to lure the spiders away from it. Adult female *Misumena* locate hunting sites primarily by the concentration of large insects at flowers (Morse 1988b).

Subjects and experimental setup.—I measured the adult carapace width of each individual used in this study and numbered its abdomen with a black Sharpie extra fine-point pen, a procedure that does not adversely affect them (Morse & Fritz 1982). Gravid adult female spiders used in this study had been placed on common milkweed *Asclepias syriaca* plants, enclosed by a 35 × 20 cm bag of white nylon tricot, shortly before building their nest on a leaf (Morse 1985) and laying their brood of eggs. I recorded laying dates and allowed the females to guard their nests on the milkweed leaves *Asclepias syriaca* for 1–26 days, the average time to emergence of *Misumena* young from their natal nests (Morse 1987). I measured and weighed these individuals immediately prior to egg-laying and weighed them again immediately after laying and before release into the patch of marjoram. I made these measurements in the laboratory, adjacent to the study area, and returned the spiders to the field immediately after weighing.

After weighing I released 20 of these post-reproductive individuals onto inflorescences in the marjoram patch in 2001 and 2004–2007, separating them from each other as much as possible. I only released 20 individuals per year because of the limited size of the test area and the number of individuals available, the latter a consequence of several other studies carried out simultaneously. Upon their release I marked each spider's position in the patch with a small flag, which allowed me to calculate the minimum distance it traveled (distance between previous and present spot) if it changed its location. I measured distances traveled because of the possibility that they would reflect differences in quality of hunting sites and hence gains in mass.

I monitored the released individuals in the patch of marjoram from 2–23 August, carefully searching the patch for the spiders every third day, weighing each individual found, measuring the minimal distance it could have traveled over that time, and replacing it in its current location, at the same time repositioning its flag to the new site if the spider had changed its location. On other days, I recorded the locations of any individuals observed, also searching the nearest goldenrod inflorescences for spiders that might have left the patch.

Sample sizes of several variables used in the analyses tallied to less than the 100 individuals released, because I did not record all of the variables from all of the individuals tested each year. Numbers ranged from 52 to 100.

I censused numbers of potential insect prey in the marjoram patch at approximately noon on every other day. The exact time of these counts varied between 11:30 and 13:00 h and depended on other projects carried on simultaneously. Prey recorded in these censuses weighed ~ 25 mg or more (bumblebees, butterflies, large sarcophagid and syrphid flies), since earlier work demonstrated that adult female *Misumena* cannot maintain their body mass on prey much smaller than these insects (Morse 1979) and that they do not choose among prey in the > 25 mg range. During 2002 and 2003, years in which I did not add post-reproductive *Misumena* to the site, I nevertheless counted the insects in the same way as in the years of spider additions.

Analyses.—I compared the among-year differences of A) percent daily loss in mass while nest-guarding (arcsin transformed) and B) percent daily gain in mass subsequent to release (arcsin transformed) with one-way ANOVAs, using proportional values to accommodate for the differences in size of the spiders. In the absence of significant among-year differences, I pooled the results from the different years in subsequent analyses. I then subjected the pooled samples to backward stepwise multiple regression analysis (Sokal & Rohlf 1995). I incorporated independent variables likely to account for differences in percent daily loss in mass during nest guarding and percent daily gain in mass after release. Initially these variables were 1) maximum mass before egg-laying, 2) mass after egg-laying, 3) mass at release into marjoram, 4) carapace width, and 5) days after laying (a measure of starvation period). After screening for collinearity ($r > 0.8$), I removed Independent Variable 2, mass after egg-laying, because of its strong correlation with Independent Variable 1, maximum mass before egg-laying.

Table 1.—Important variables of adult female crab spiders *Misumena vatia* used in this study.

Variable	n	Mean ± SE	Range
Maximum mass before laying (mg)	99	221.4 ± 5.99	114.8–365.7
Mass immediately after laying (mg)	81	74.8 ± 2.08	42.0–125.8
Mass at release into foraging site (mg)	100	68.6 ± 1.73	39.5–110.0
Time guarding after laying (days)	99	13.6 ± 0.68	1–26
Carapace width (mm)	100	3.4 ± 0.03	2.8–4.0
Distance moved (cm)	52	89.0 ± 8.42	9–244

Following a one-way ANOVA to test for between-year differences, I compared percent daily gain in mass with movement about the marjoram patch with a two-tailed paired t-test. Amount of movement might reflect an inability to find high-quality hunting sites (Morse & Fritz 1982). Since I could not find several individuals subsequent to their release in the marjoram patch, I tested for possible differences in numbers of missing individuals among years, using a G-test of independence. I then compared the two groups (recorded, not recorded) for possible differences in the set of independent variables noted immediately above, as well as percent daily loss of mass after egg-laying, using t-tests for the difference between two means. I looked for differences in large prey abundance among years using a G-test for goodness of fit, followed by a search for possible among-year differences in numbers of spiders recorded and prey numbers in the marjoram patch, using a t-test for paired comparisons. Such an outcome could result from differences in numbers of large insect prey. Means are reported ± SE.

RESULTS

Loss in mass during guarding stage.—I found no among-year differences in percent daily loss in mass during the nest-guarding stage (one-way ANOVA: $F = 1.98$; $df = 4, 72$; $P > 0.1$); thus, I pooled years in analyses of loss in mass. Of the several variables potentially related to percent daily loss in mass over the pre-release period (Table 1), time since laying and maximum pre-laying mass differed significantly in a stepwise multiple regression analysis (Table 2). The significant negative relationship between time since laying and rate of loss in mass resulted from the rate of loss decreasing over time (Fig. 1), and the weaker positive relationship (Fig. 2) resulted from larger individuals losing mass at a proportionately greater rate than the smaller ones. Other measures directly related to mass (mass at release into marjoram, carapace width) did not differ significantly (Table 2). The 19 individuals retained more than 20 days after egg-laying lost 17.3 ± 1.53% of their body mass, with a maximum of 28.4%.

Table 2.—Parameter estimates from a multiple regression model by standard least squares of percent daily loss in mass (arcsin transformed) of adult female *Misumena vatia* in relation to several variables. Model summary: $n = 77$, $R^2 = 0.18$, $F = 3.81$, $P < 0.01$.

Variable	Partial regression coefficient	Standard error	t	P
Intercept	2.497	0.921	2.71	< 0.01
Maximum mass before egg-laying	0.003	0.002	2.13	< 0.05
Mass at release	− 0.005	0.006	− 0.85	> 0.3
Carapace width	− 0.500	0.375	− 1.33	> 0.1
Days after laying	− 0.028	0.009	−3.03	< 0.0

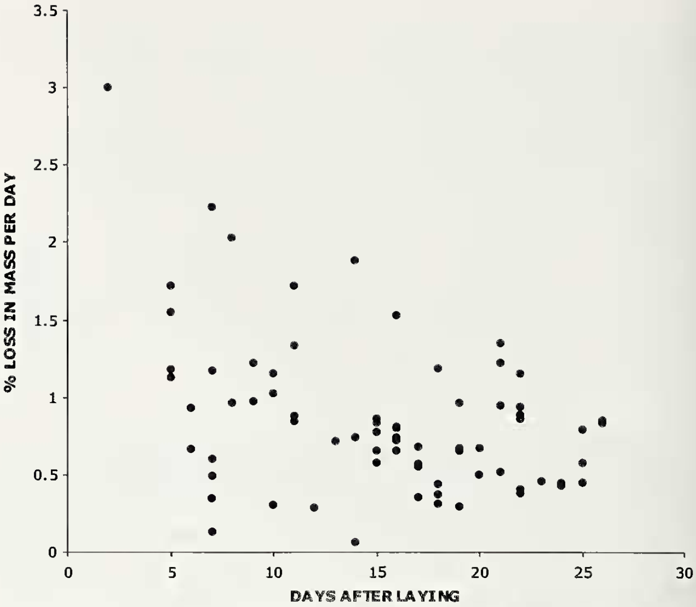

Figure 1.—Percent daily loss in mass of female crab spiders after laying brood of eggs. Mass measured immediately after eggs laid and at time of removal from nest for deployment to marjoram.

Gain in mass after release.—Testing the same variables as in the preceding section in the same way, I found no among-year differences in percent daily gain in mass subsequent to release of the post-reproductive spiders into the marjoram patch (one-way ANOVA: $F = 2.27$; $df = 4, 59$; $P > 0.05$). None of these variables exhibited a significant relationship with percent daily gain in mass subsequent to release in a stepwise multiple regression analysis (Table 3). Perhaps surprisingly, given the effect of time since laying on loss in mass, this variable did not significantly differ from gain in mass after release (Table 3).

Movement of individuals recorded after release.—I found no between-year differences in minimum distances moved in the patch of marjoram after release during the 2004–2007 seasons

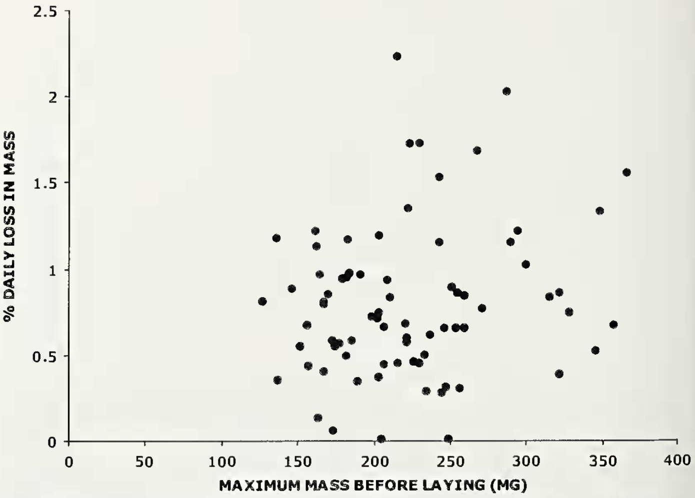

Figure 2.—Percent daily loss in mass of female crab spiders in relation to maximum pre-laying mass.

Table 3.—Parameter estimates from a multiple regression model by standard least squares of percent daily loss in mass (arcsin transformed) of adult female *Misumena vatia* in relation to several variables. Model summary: $N = 64$, $R^2 = 0.08$, $F = 1.20$, $P > 0.3$.

Variable	Partial regression coefficient	Standard error	t	P
Intercept	− 1.185	5.864	− 0.20	> 0.8
Maximum mass before egg-laying	0.013	0.011	1.19	> 0.2
Mass at release	− 0.030	0.037	− 0.81	> 0.4
Carapace width	1.491	2.370	0.63	> 0.5
Days after laying	0.013	0.058	0.22	> 0.8

(one-way ANOVA: $F = 0.25$; $df = 3, 47$; $P > 0.8$). (I did not record this variable in 2001.) The spiders varied greatly in the minimal distances traveled within the marjoram patch (9–244 cm); however, distance moved bore no relationship to percent gain in mass per day ($t = -0.19$, $df = 51$, $P > 0.8$ in a two-tailed paired t-test).

Individuals recorded after release.—I failed to find several spiders subsequent to their release (20 released each year), though the numbers of individuals seen after release varied among years (12, 9, 10, 16, 17: $G = 11.59$, $df = 4$, $P < 0.05$ in G-test of independence). Almost all the observed individuals occupied hunting positions among the flowers, notwithstanding the considerable effort expended in search. Since I often found temporarily missing individuals in subsequent searches, they apparently spent considerable periods in the dense, lower parts of the vegetation, away from the terminal flowers that attracted potential insect prey. I missed some individuals for two or three surveys in a row, only for them to appear on a later date. Although this uncertainty makes it difficult to calculate emigration rates from the marjoram patch, systematic searches of the nearby vegetation yielded only a single individual, found on goldenrod, over the five years. I returned that individual to its previous position in the marjoram patch, but subsequently found it away from the patch in goldenrod a second time.

No significant difference occurred between individuals recorded and not recorded after release in any of the variables measured (Table 4). They did not even differ in days since laying, a measure of post-reproductive age (those found = 13.4 ± 0.86 days, $n = 64$; those not found = 14.0 ± 1.16 days, $n = 36$).

Influence of large insect visitors.—Data on visits by large insect prey exist for the five years in which I monitored the spiders, plus 2002 and 2003 (Fig. 3). Numbers of insects differed widely among years ($G = 479.98$, $df = 6$, $P < 0.001$ in a G-test for goodness of fit. However, no relationship emerged between numbers of large insects visiting the flowers (bumblebees, butterflies, large flies) and the number of spiders seen once or more after their release ($t = -0.66$, $P > 0.5$ in a two-tailed t-test for paired comparisons). Percent daily gain in mass of these spiders varied only between 5.1 and 6.1, except for 3.7 in 2007, while numbers of large insects differed nearly six-fold over the census period. The higher proportion of spiders subsequently recorded in 2006 and 2007 (16 and 17 of 20) occurred during years of relatively low insect visitation, but those individuals were recorded in the marjoram for a length of time that did not differ markedly from the earlier years (mean = 10.0 days; range of 8.3–12.6 days over the total years of the study).

Table 4.—Characteristics of individuals recorded after release in marjoram patch and those not recorded after release. Sixty-four of the one hundred individuals were subsequently recorded. Two-tailed t-tests.

Factor	Number	t	P
Maximum body mass	98	−1.391	> 0.1
Body mass after egg-laying	80	−0.453	> 0.6
Body mass at release	99	−1.198	> 0.2
Days since laying	100	+0.445	> 0.6
Carapace width	99	−0.377	> 0.7
% loss/day after egg-laying	76	−0.682	> 0.4

DISCUSSION

Changes in mass.—Only the number of days since a spider had laid its brood, a likely correlate of how recently it had fed, and mass immediately before egg-laying significantly affected percent daily loss in mass subsequent to egg-laying. Although individuals naturally continued to lose mass, the rate of loss decreased over time, probably reflecting a decrease in metabolic rate. Anderson (1974) demonstrated that the metabolic rate of both *Hogna lenta* (Hentz 1844) and *Kukulcania hibernalis* (Hentz 1842) declined within a few days under starvation conditions in the laboratory, and it is reasonable to propose a similar pattern for *Misumena* as well. The greater rate of loss in mass of the larger individuals should reduce advantages they might gain over smaller individuals, either for survival or for conversion into offspring in a possible second brood. However, large individuals presumably have more resources to use in such a situation than small ones. As a

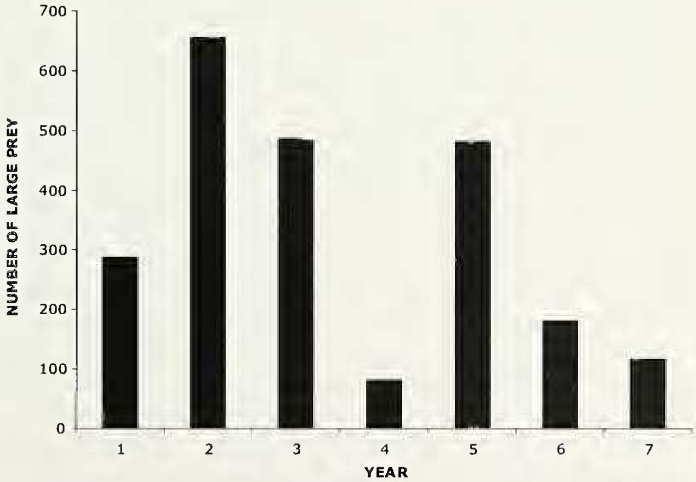

Figure 3.—Cumulative numbers of large prey (bumblebees, butterflies, large flies) at marjoram patch in noontime censuses over period of study in years 2001–2007 (##1–7).

consequence of their change in rate of loss in mass, my post-reproductive individuals probably did not lose enough mass to endanger their survival over the maximum time tested, 26 days, a period that matched the mean time between egg-laying and emergence of spiderlings from their nest sac (Morse 1987). The percent loss in mass of the individuals retained the longest (20 days or more) fell well below the 35–40% lost by post-reproductive female *Misumena* before succumbing (Morse 1987).

None of the variables tested significantly affected percent daily gain in mass among the released individuals. This lack of relationship to any of the variables contrasts strikingly with pre-oviposition gain in mass, for which strong correlations existed between gain in mass and key independent variables (Morse & Fritz 1982; Fritz & Morse 1985). The failure of the spiders to respond to the wide fluctuation in numbers of prey suggests that enough insects always visited the flowers that their abundance did not become an important factor in gaining mass for the spiders. The fluctuation in prey numbers was most likely ultimately driven by outbreaks of goldenrod beetles *Trirhabda* spp., which defoliated much of the surrounding goldenrod (Morse 2007), thereby reducing the major resources of the pollinators in the field and, hence, the food supply of the spiders.

Individuals recorded and not recorded after release.—Earlier studies on post-reproductive female *Misumena* retained in the same way as in this study (Morse 1994) revealed that of the individuals abandoning their nests over a 26-day period (45% of the total), half had died, and half had moved to other parts of the bags (they presumably would have dispersed if given the opportunity). That result suggests that several of the missing individuals died in the marjoram patch during the observation period, although I found no dead ones. Further, the missing individuals did not differ significantly in traits measured prior to release from those subsequently observed.

The general failure to find released spiders outside the marjoram patch, even on the nearest flowers, suggests that they seldom left the release site, a behavior similar to that of prereproductive adult females at rich hunting sites (Morse & Fritz 1982). Although anecdotal, the recovery of a single individual outside the patch, followed by a repeat recovery of that same individual outside the patch shortly after I returned it to its previous site in the patch, further suggests that I seldom failed to find individuals that had quit the site. Even though a high density of conspecifics in the patch might engender dispersal, prereproductive adult female *Misumena* not infrequently reach similar densities at sites with extremely high rates of prey visitation (Morse 2007).

Relationship to semelparity.—This data set is notable for the dearth of significant correlations observed, especially in post-reproductive gain in mass, consistent with the predictions of Fisher (1930), Williams (1957), and subsequent workers. The few significant relationships involved loss in mass prior to release and resembled the success enjoyed by individuals during the prereproductive part of the life cycle, a likely consequence of advantages accruing to individuals at that stage (Morse & Stephens 1996). These post-reproductive performances likely do little or nothing to enhance selection for producing a second brood.

Post-reproductive *Misumena* thus perform very much like semelparous forms, exhibiting few characteristics that would attain high fitness values if employed earlier in life. In themselves these properties should favor the evolution of semelparity, with progressively higher allocation to egg production. However, parental nest defense has high survivorship value for the young in these *Misumena* populations (Morse 1988a), which should counter selection to yet higher reproductive effort (% body mass devoted to brood) (Tallamy & Brown 1999). These spiders already exhibit an extremely high reproductive effort, in itself a trait exhibited by semelparous individuals (Roff 2002; Stearns 2002), relative to that of co-occurring species with comparable nesting strategies (Morse 2007). The extremely low resting metabolic rate of spiders (Anderson 1970) may facilitate nest guarding under conditions that favor semelparity. It may also facilitate their ability to lay a second brood as large as the first under experimental conditions (Morse 1994), although if individuals in the wild were constrained to lay large second broods, this trait should make iteroparity an even greater obstacle. Thus, characteristics that facilitate more than a random opportunity to become functionally iteroparous appear to be lacking in this population of *Misumena*.

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